

Interactive effects of fearfulness and geographical location on the population trends of breeding birds

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Abstract

Animal populations are currently under pressure from multiple factors that include land use and climate change. They may adapt to such effects by reducing the distance at which they flee from humans (i.e., flight initiation distance, FID), consequently modifying their population trends. We analyzed population trends of common breeding birds in relation to FID and geographical location (latitude, longitude, and marginality of the breeding distribution) across European countries from Finland in the north to Spain in the south, while also considering other potential predictors of trends like farmland habitat, migration, body size and brain size. We found evidence of farmland, migratory and larger-sized species showing stronger population declines. In contrast, there was no significant effect of relative brain size on population trends. We did not find evidence for main effects of FID and geographical location on trends after accounting for confounding and interactive effects; instead, FID and location interacted to generate complex spatial patterns of population trends. Trends were more positive for fearful populations northwards, eastwards and (marginally) towards the centre of distribution areas, and more negative for fearless populations toward the south, west, and the margins of distribution ranges. These findings suggest that it is important to consider differences in population trends among countries, but also interaction effects among factors, because such interactions can enhance or compensate for negative effects of other factors on population trends.

Keywords: European breeding birds; farmland; flight initiation distance; latitude; marginality of distribution; migration; population trend.

Introduction

Human disturbance of wild organisms is a common cause of concern in a world with a rapidly increasing human population (e.g. Wong and Candolin 2012; Ehrlich and Ehrlich 2013). Such effects of disturbance include release of stress hormones (e.g. Wingfield and Ramenofsky 1999), increased metabolic rate (e.g. Belanger and Bédard 1990), reduction in foraging activity (e.g. Madsen 1998a, b), disturbance from hunting (e.g. Madsen 1988a, b) and non-lethal effects of predation (e.g. Abrams 1991). These factors on their own and in combination may have effects on the condition of animals and hence on their reproduction and survival prospects. A common behavioral measure of proneness to disturbance by humans and animals alike is the flight initiation distance (FID): The distance at which an animal takes flight when approached by a potential predator (Cooper and Blumstein 2015). Because all animals continuously have to weigh the risk of falling prey to a predator by fleeing when approached against the benefits of staying put and hence continuing to feed and/or rest, FID constitutes an instantaneous measure of this individual trade-off. Cooke (1980) noticed that urban birds had much shorter flight distances than rural populations of the same species, and that this difference depended on body size, the difference being larger in small species with high metabolism. This change in behavior between urban and rural habitats allowed birds to coexist with humans even at high human population densities that is a cause of frequent disturbance. Parallel latitudinal trends in FID and raptor abundance (Díaz et al. 2013) suggest that birds also adjust their behavior in response to natural levels of disturbance by predators.

Burger (1981), Burger & Gochfeld (1981) and several others noticed that human disturbance at seabird colonies linked to escape behavior and FID could result in altered habitat use and reduced reproductive performance. Therefore, FID can be a useful tool in conservation including assessment of levels of disturbance and susceptibility to disturbance (e. g. Madsen, 1995, 1998a, b; Weston et al. 2012). The population consequences of FIDs can be investigated by

relating population trends to FID (Møller 2008b). We should expect species with long FIDs for their body size to show declining population trends because such species should be more prone to get disturbed by humans. Among 56 species of birds, FID accounted for 33% of the variance in population trends in Denmark, with effect sizes ranging from 0.36 to 0.58 in different analyses. Therefore, species with long FIDs for their body size had declining populations while species with short FIDs had increasing populations even when controlling statistically for potentially confounding effects. Thaxter et al. (2010) analyzed population trends in the UK in relation to predictors that included FID recorded in Denmark, but found no significant relationship between FID and population trends. This raises the question whether population trends and FID should originate from the same geographic location to make analyses meaningful.

Many national and international monitoring programs tally population trends of organisms as diverse as birds, mammals, butterflies and bumblebees. In particular, birds have been popular targets for monitoring since the 1960's in many countries in Europe, and population trends based on European continent-wide monitoring have been published since 1980 (European Bird Census Council, <http://www.ebcc.info/index.php?ID=509>). According to these data, while many species have increased in distribution and abundance, a majority, at least in specific habitats such as farmland, have shown a clear decline. Although humans either directly or indirectly play a major role in determining long-term population trends of birds in Europe (Reif 2013), the underlying mechanisms remain poorly understood. In addition, population trends vary intraspecifically. Cuervo and Møller (2013) found stronger increases in northern populations and greater fluctuations in marginal populations, somewhat expected from influences of global warming on climatic niches (Hampe and Petit 2005), and Donald et al. (2001) and Reif et al. (2011) showed longitudinally varying trends. Reif et al. (2011) also showed an interesting difference in the effect of relative brain size on trends at both sides of the iron curtain, consistent with the differences in land-use

intensity across Europe. These intriguing and varying patterns, and the need to optimize conservation priorities, mean that there are good reasons to investigate patterns of population trends at different spatial scales in an attempt to elucidate the underlying mechanisms including the potential effects of FID.

The objectives of this study were to test whether population trends were related to FID, and whether these influences varied across the European continent. If spatial changes in FID could partially compensate for the main effects of factors of global change on trends, we predicted significant interactions between FID and latitude, longitude and marginality on trends. We also tested whether previously established predictors of population trends such as farmland habitat, migration distance, body mass or brain mass affected the relationship between population trend and FID. Overall, geographical variation in the relationships between trends and recent responses of organisms to changes in the level of human activities will help to understand our impact on wild populations of animals and eventually to reduce such impacts.

Materials and methods

We recorded FID for a total of 159 species during the breeding seasons 2009-2010 at nine locations from eight countries along a wide latitudinal gradient across Europe, from Finland in the north to Spain in the south, by using a standard procedure developed by Blumstein (2006). These data are reported in Díaz et al. (2013). In brief, we walked at ordinary walking speed towards a bird recording the distance from the bird when we started walking, the distance at which the birds initiated escape, and the bird's height in the vegetation. This information was used to estimate FID. In order to account for the height at which individuals were perched, FID was calculated as the Euclidean distance between the approaching human and the focal bird (which equals the square-root of the sum of the squared flight distance and the squared height in the vegetation). Observers wore neutrally colored clothes and behaved as normal pedestrians.

FID was measured by a number of trained observers and therefore data were pooled for analysis. We used the FID estimates for rural populations in each location (that consisted of paired rural and urban sites; Díaz et al. 2013), because the population size estimates used to assess trends for each country are mostly based on data coming from non-urban populations (Cuervo and Møller 2013). Data for the two Spanish sites were averaged to obtain a single country-level estimate.

We obtained from Cuervo and Møller (2013) the population trends for breeding birds in all European countries for which we had information on FID: Finland, Norway, Denmark, Poland, Czech Republic, Hungary, France and Spain. Available population size estimates for each bird species and country were regressed on years, and the slope of this regression was used as a proxy for population trend (Cuervo and Møller 2013).

Latitude and longitude of bird populations in each country were estimated as the coordinates of the mid-point between the northernmost and the southernmost, and between the easternmost and the westernmost, mainland points of the breeding range of every country, excluding islands except for Denmark. Marginality of each bird population was estimated using the distance (L) in degrees between the breeding population latitude and the northernmost or the southernmost (the one that resulted in a shorter distance) limits of the breeding distribution range of the species and the distance (C) in degrees between the population latitude and the latitude of the mid-point between the northernmost and the southernmost limits of the breeding distribution range of the species according to the equation $\log_{10}(C+1) - \log_{10}(L+1)$, with positive values representing marginal populations and negative values central populations. These values were transformed by adding the absolute value of the most negative number and dividing by the largest value resulting from the previous addition, to ensure that marginality estimates ranged from 0 (central population) to 1 (marginal population; see Cuervo and Møller 2013 for details).

Bird population trends have previously been shown to be systematically affected by body size, migration distance, farmland habitat and relative brain size (reviews in Møller 2008a, Møller et al. 2008, Reif 2013). We extracted information on mean body mass of adult birds of each species from Cramp & Perrins (1977-1994). Migration distances (mean of the northernmost and the southernmost latitudes of the breeding distribution range minus the corresponding mean for the wintering distribution range) were taken from Møller et al. (2008). Farmland habitat was coded as 1 (species depending on arable and/or mixed farmland) or 0 (species depending on other habitat types) following Appendix 2 in Tucker and Evans (1997). Relative brain sizes were the residuals of a log-log phylogenetically corrected regression of brain mass on body mass based on a sample of 567 bird species (Møller 2008a); brain mass data were obtained from Iwaniuk and Nelson (2002), Møller and Erritzøe (2014), Galván and Møller (2011) and Garamszegi et al. (2002).

We \log_{10} -transformed FID, population trend and migration distance before analyses. Within-species repeatability of FID and trends across Europe was computed following Lessells and Boag (1987), and differences between them and the null hypothesis of zero repeatability were tested following Becker (1984). Significant repeatabilities imply statistical dependence of estimates for the same species in different countries, a fact that will bias results based on phylogenetically-structured databases (Garamszegi and Møller 2010). As species occupy a variable number of study locations and countries (Cuervo and Møller 2013, Díaz et al. 2013), geographical trends could be partly due to phylogenetic effects. To control for such relationships we used phylogenetic generalized least square regression (PGLS) models implemented in R (see Díaz et al. 2013 for a similar approach). After estimating the phylogenetic scaling parameter lambda (λ), we calculated the phylogenetically corrected partial correlations between the variables of interest. Different populations of the same species were considered as polytomies with a constant small genetic distance of $1 \cdot 10^{-10}$ between them. We

used the R script and the edited phylogeny supplied as Supplementary Files S1 and S2 in Díaz et al. (2013), but using the function *pglm3.3.r* instead of the *pglm3.1.r* to fit type III (orthogonal) models. The dependent variable was the population trend, confounding variables were farmland habitat, migration distance, body size and relative brain size, and predictors FID, latitude, longitude, marginality, and the first-order interaction between FID and geographical variables. Predictors were computed from the corresponding input variables (\log_{10} FID and geographical variables) by standardizing them (i.e., by subtracting sample means and dividing by standard deviations), in order to allow direct comparison of effect sizes (computed from P values of t-tests according to Lipsey and Wilson 2001) and to make main effects biologically interpretable even when involved in interactions (Schielezeth 2010). The magnitude of associations between trends and predictor variables was estimated as their effect sizes,

Results

We collected data on mean FID and on recent population trends from 338 populations of 129 bird species. Data on farmland habitat, body size and migration distance were available for all them, while there were no data on brain size for 9 species (Supplementary Table 1). Both FID and trends were significantly repeatable within species ($F_{1, 209} = 3.08$, $P < 0.001$ and $F_{1, 209} = 1.45$, $P = 0.009$, respectively). FID was significantly more repeatable than population trends ($r = 0.45 \pm 0.04$ (SD) vs. $r = 0.15 \pm 0.05$; $t_{338} = 4.0$, $P < 0.001$; Becker 1984); in other words, geographical variation within species was larger for population trends than for mean fearfulness as reflected by FID.

Log-transformed population trends were significantly related to \log_{10} FID ($F_{1, 337} = 7.96$, $P = 0.005$, $r^2 = 0.02$), but not to latitude ($F_{1, 337} = 0.00$, $P = 0.967$, $r^2 = 0.00$), longitude ($F_{1, 337} = 0.40$, $P = 0.530$, $r^2 = 0.00$) or marginality ($F_{1, 337} = 0.62$, $P = 0.432$, $r^2 = 0.00$). The relationship vanished, however, after correcting for significant effects of farmland habitat, migration distance and body mass

(effect sizes from 0.14 to 0.16), while also accounting for phylogenetic effects (Table 1). Trends were more negative for farmland birds, long-distance migrants and smaller species (Table 1). Relative brain size showed no significant effects on population trends, which did not show significant geographical trends either (Table 1). However, FID showed significant interactive effects with latitude, longitude and marginally, with effect sizes ranging from 0.10 to 0.13 (Table 1, Fig. 1). FID-trend relationships were more positive northwards, eastwards and (marginally) towards the centre of distribution areas (Table 1, Fig. 2). These interactions implied that trends were more negative for fearless populations toward the south, west, and the margins of distribution ranges.

Discussion

Many different factors have been proposed to account for population trends of birds (reviewed in Reif, 2013). These variables range from migration and the perils of living under different climate regimes (Hjort and Lindholm, 1978; Baillie et al., 1992; Sanderson et al., 2006; Reif, 2011), relative brain mass that facilitates the ability to cope with changing environments (Shultz et al., 2005; Møller et al., 2008; Reif et al., 2011), thermal range and hence the ability to cope with changing climatic conditions (Jiguet et al., 2007), the number of broods with species producing more broods doing better (Julliard et al., 2004), and body mass with large sized species with smaller total populations having negative population trends (Bennett and Owens, 2002).

Geographical variation in trends within breeding ranges of species are also to be expected due to geographical changes in the suitability of environmental conditions (the niche variation hypothesis; Brown 1984), in the intensity of global change drivers (Hampe and Petit 2005, Reif et al. 2011, Tryjanowski et al. 2011) or both (Díaz et al. 1998). Cuervo and Møller (2013) have recently shown that changes in population size of breeding birds in Europe are the strongest at the margins of the breeding distribution, but are particularly negative at the southern-

most range margins, where increasing temperatures may render environmental conditions for maintenance of viable populations the most difficult. Climate change has affected the distribution of many species, and range margins have on average moved pole-wards (e.g. Chen et al., 2011). Longitudinal variation due to differences in land-use intensity between Western and Eastern Europe have also been documented, especially for farmland birds (Donald et al. 2001). However, we did not find evidence for direct effects of these variables after accounting for effects of third variables and their interactions. We hypothesized that effects of longitude would be stronger towards the west where agriculture and forestry is more industrialized than in the east. In fact, Reif et al. (2011) suggested that the iron curtain dividing industrialized Western Europe from more extensive land use in Eastern Europe as one factor accounting for spatial heterogeneity in population trends, together with relative brain mass. Here we found no evidence of an effect of relative brain mass on population trends contrary to previous reports (Shulz et al. 2005; Thaxter et al. 2010; Reif et al. 2011). We hypothesize that these differences among studies may arise from the inclusion of different predictors and their interactions, but also from inclusion of multiple countries that differ in significant predictors of population trends.

Bird species breeding on farmland displayed the steepest declines. This is probably a consequence of agriculture having become ever more industrialized and intensified and thereby disproportionately negatively affecting farmland specialists (Fuller et al., 1995; Chamberlain et al., 2000; Møller et al., 2008; Reif, 2013). Here we found evidence consistent with this general trend with farmland species showing strong population declines. Migration has been predicted to affect population trends because migrants are affected negatively by land-use and climate change in their breeding range, during migration and in their winter quarters (Hjort and Lindholm, 1978; Baillie et al., 1992; Sanderson et al., 2006; Møller et al. 2008; Reif, 2013). Here we found a negative effect of migration

distance on population trends, when accounting for the effects of the remaining variables.

We hypothesized that population trends would be negatively related to FID, as reported by Møller (2008a) for European birds. We found an overall main effect of FID in this study, that however vanished when considering phylogenetic and interactive effects with geographical location. This fact suggests that the observed geographical variation in trends would in fact be the net result of complex interactions between spatial variation in many factors proposed to drive populations trends (Reif, 2103). Our results showed that fearfulness of bird populations (i.e., long FIDs) enhanced population trends where such trends were already less negative (northern and eastern European populations ; Cuervo and Møller 2013, Tryjanowski et al. 2011), but this relationship reversed at more stressful extremes of spatial gradients, such as southern, western and marginal locations. We interpret these interactions as implying that we cannot assess predictors by considering solely their main effects. We are unaware of any previous studies investigating such interaction effects as predictors of population trends. Finally, we note that the effect of FID remained after inclusion of body mass as a predictor of population trends. Large species are generally more threatened than small species (Bennett and Owens 2002). However, large species also have longer FID than small species. Therefore, we conclude that species with a relatively long FID and hence species that are easily disturbed by humans show declining population trends, especially at low latitudes and eastern and marginal locations of their breeding distribution ranges, where tolerance to disturbance would be positively selected.

In conclusion, we have analyzed for the first time how geographical patterns of population trends of birds in Europe are related to natural and man-made geographical variation in environmental factors such as climate, predation risk and land use, and how they interact with a measure of the tolerance of birds to human disturbance. Overall we found that proneness to risk-taking as

estimated by short FIDs enhanced population resilience to disturbance in a changing world, as more tolerant individuals will reduce the costs associated with escape behaviors (Cooper and Blumstein 2014). In contrast, bird species and populations less tolerant of frequent disturbance, by humans or wild and domestic predators would perform worse, especially at the southern-most edges of breeding distributions.

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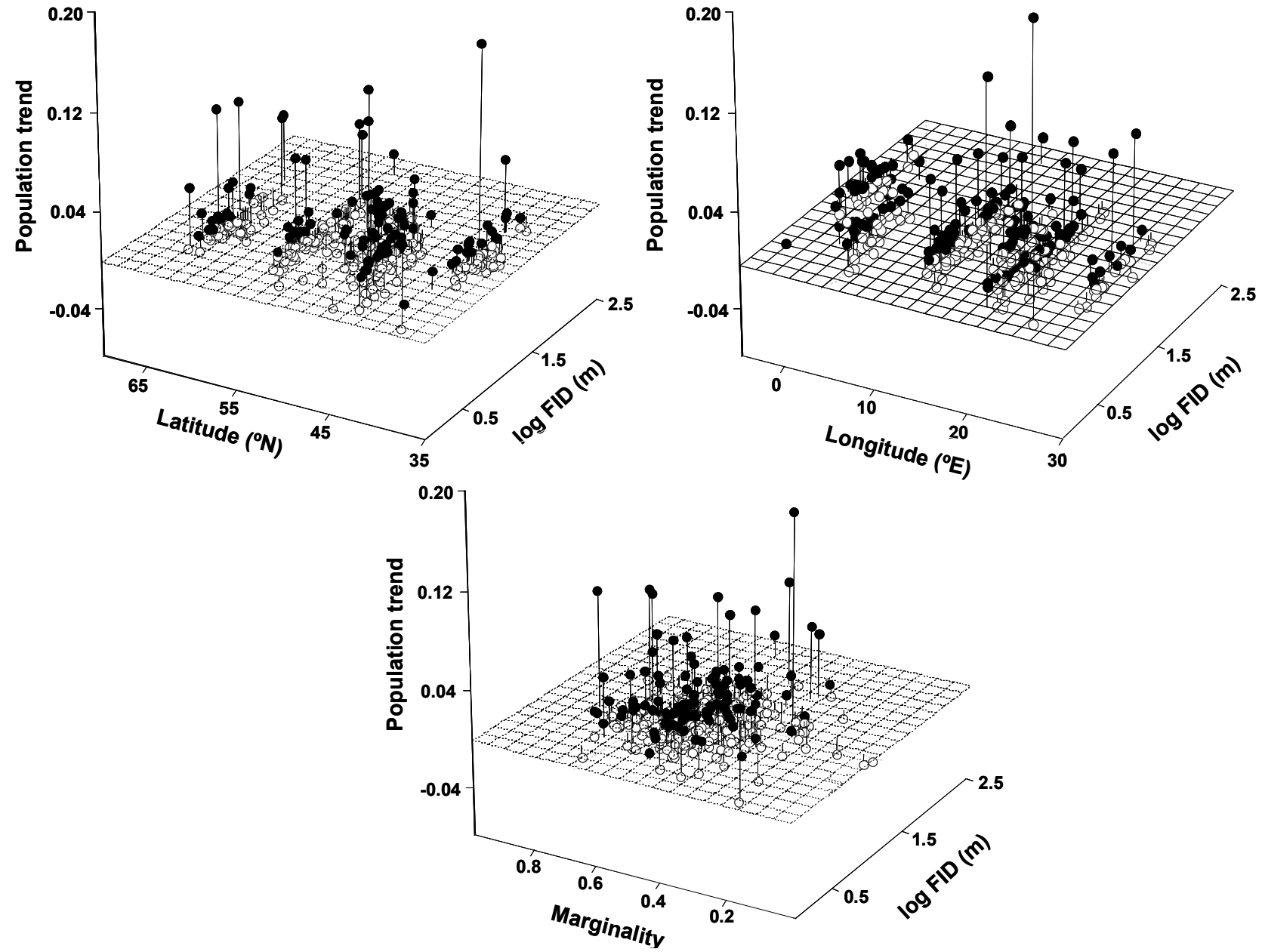
Legends to figures

Fig. 1. Relationship between population trends of European birds and fearfulness (flight initiation distance, FID, log-transformed), and latitude (left), longitude (right) and marginality (bottom). Trend data are the residuals from a multiple regression between log-transformed trends, migration distance, body mass, relative brain mass and farmland habitat. Planes represent best-fitted multiple regression models. Filled symbols are located above the planes and open symbols below.

Fig. 2. Latitudinal and longitudinal variation in standardized regression coefficients ($\beta \pm \text{SE}$) between population trends of European birds (residuals from a multiple regression between log-transformed trends, migration distance, body mass, relative brain mass and farmland habitat) and fearfulness (flight initiation distance, FID, log-transformed). Lines are best-fit regressions.

494 Fig. 1

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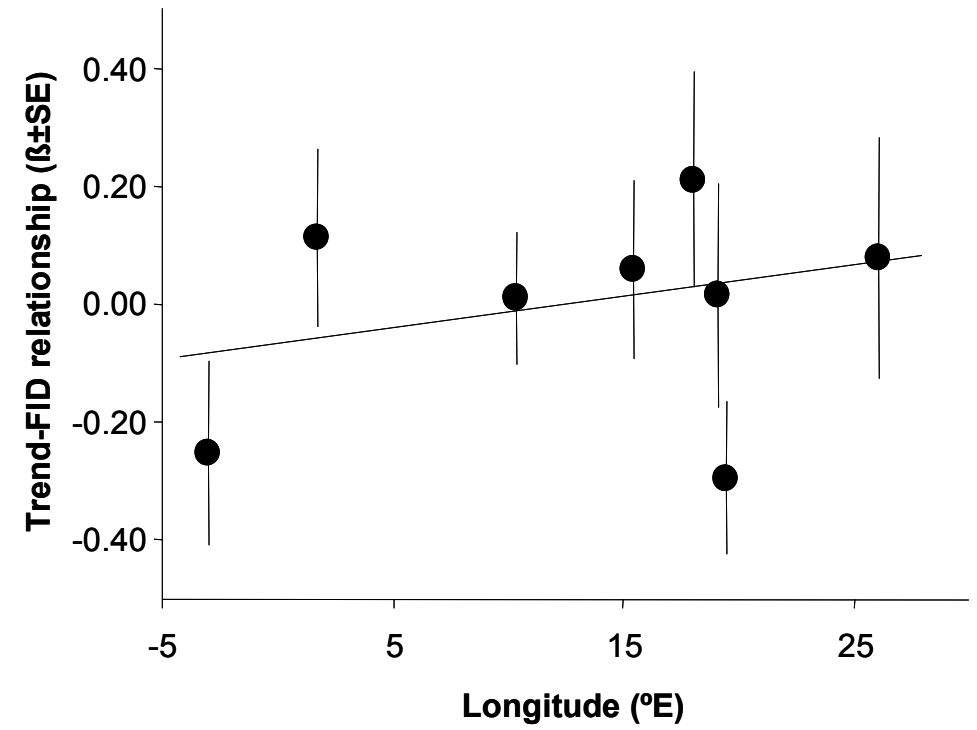
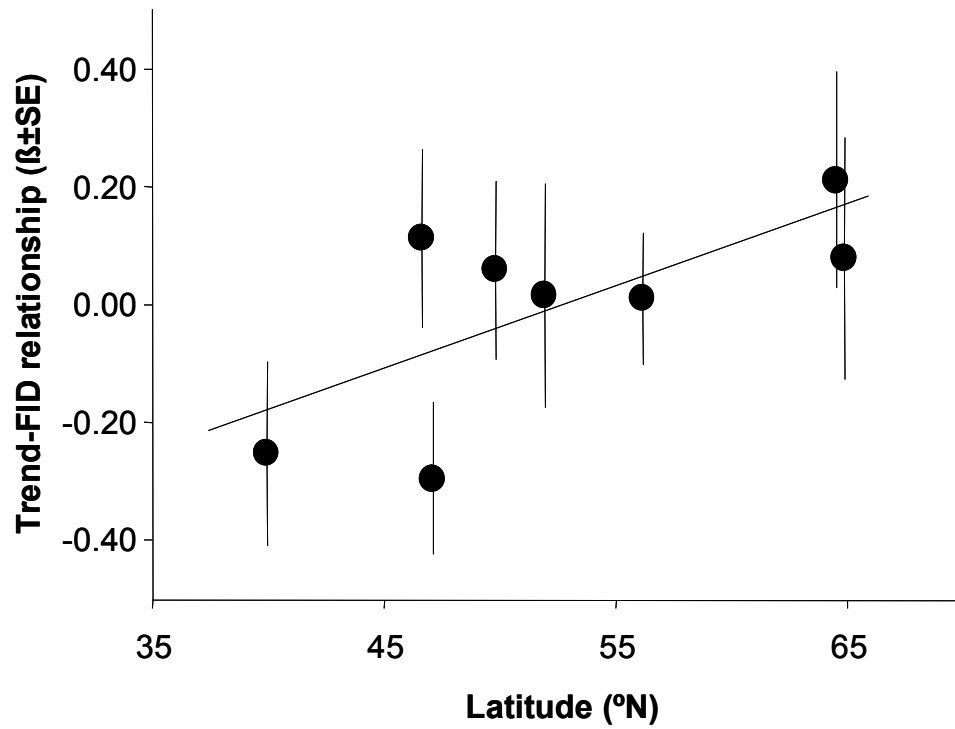
496 **Fig. 2.**

Table 1. Relationships between population trends of European birds (response variable) and geographical location (latitude, longitude and marginality) and fearfulness (flight initiation distance, FID), after accounting for effects of farmland habitat, migration distance, body mass and relative brain size on trends and correcting for the effect of the phylogenetic structure of the data set, that was, however, not significant ($\lambda = 0.000$, $\chi^2 = -0.012$, $P = 1.000$). The full model (no removal of non-significant terms as recommended by Forstmeier and Schielzeth 2010) had the statistics $F = 4.73$, d.f. = 12, 329, adjusted $r^2 = 0.11$, $P < 0.0001$. Effect sizes are Pearson's product-moment correlation coefficients.

Source	estimate (SE)	<i>t</i>	<i>P</i>	Effect size
Farmland	-0.008(0.003)	-2.50	0.013	0.14
Migration distance	-0.006(0.002)	-2.71	0.007	0.15
Body mass	0.018(0.006)	2.93	0.004	0.16
Relative brain size	-0.014(0.010)	-1.46	0.147	0.08
FID	0.000(0.002)	0.16	0.876	0.01
Latitude	-0.002(0.002)	-1.07	0.286	0.06
Longitude	0.003(0.002)	1.50	0.134	0.08
Marginality	0.001(0.002)	0.38	0.706	0.02
FID x Latitude	0.005(0.002)	2.29	0.023	0.13
FID x Longitude	-0.004(0.002)	-2.27	0.024	0.12
FID x Marginality	-0.003(0.002)	-1.76	0.079	0.10